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THE GUEST ANT, *SYMMYRMICA CHAMBERLINI*, REDISCOVERED NEAR SALT LAKE CITY, UTAH (HYMENOPTERA, FORMICIDAE)*

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Introduction

In a series of recent papers we investigated the social structures of *Formicoxenus nitidulus, F. hirticornis,* and *Leptothorax provancheri* (Buschinger und Winter 1976, Buschinger 1979, Buschinger, Francoeur and Fischer 1980). They are all so-called guest ants, small species living in independent colonies within the larger nests of their host species. *Formicoxenus* gains its food by soliciting it from the *Formica* hosts, or by stealing food when two *Formica* workers feed each other (Stäger 1925, Buschinger 1976). *L. provancheri* are often seen licking the head and body of their *Myrmica* hosts; however, it remains uncertain how they really get their food. Our observations revealed that these guest ants had some interesting features in common, such as a functional monogyny, a queen polymorphism with dealate and intermorphic females, and a tendency to mate within or on the upper surface of the host nest. The *Formicoxenus* species recognized up to now have wingless, workerlike males, whereas the *L. provancheri* male exhibits an ordinary winged shape.

It was a challenging task, therefore, to search for *Symmyrmica chamberlini* Wheeler (1904), another guest ant with wingless males and living together with *Manica mutica*, in order to study its biology and to find out its relationship to the species mentioned above. We took the opportunity of visiting the type area of *S. chamberlini* in the vicinity of Salt Lake City, Utah, after the 9th Congress of IUSSI in Boulder, Colorado. We were able to rediscover this ant and to collect some new material which yielded additional support for an incorporation of *Symmyrmica* into *Formicoxenus.*

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Species transferred now in Formicoxenus

Field Observations and Collecting Site

The original description of Wheeler (1904) indicates the type locality only inaccurately as "near Salt Lake City, Utah, in the flood-plains of Jordan River", where the host species, *Manica mutica*, was said to be common in some localities. *S. chamberlini*, however, was found only in one particular ten-acre field and, despite an intensive search, in no other locality. Unfortunately Wheeler's paper (1904) contains no further details on the exact site of that field.

On August 15, 16 and 17, 1982 we located about 30 flourishing *Manica mutica* populations along the Jordan River, beginning with our search near Lehi and working down the river to North Salt Lake. We followed the roads and highways crossing the river, and, always beginning at the bridges, we looked for the host species in or near the banks. *M. mutica* was found near Lehi, on the eastern bank north of the bridge of road no. 73, and in several places in West Jordan (between 5400 South Street and 7800 South Street, east bank), in Murray and South Salt Lake (between 5300 and 3300 South Street). Often the colonies seemed loosely concentrated. A search in Big Cottonwood Canyon was not successful. We have heard since then that unfortunately, late in following September, the Jordan River heavily flooded the type area, the only known nesting site for *S. chamberlini*.

The species was detected only in one locality, on the eastern bank of the river, about 200 m south of the bridge of 3300 South Street, South Salt Lake. *Manica mutica* there forms large nests in the silty soil just in the upper edge of the steep river-bank about 2 m above the waterline. The area is a horse pasture with poor, short vegetation, which was quite dry in August. Between two nests containing *chamberlini* there was a willow brush, and in the estate adjoining to the north, some rose bushes covered partly a private garbage dump. One very large *mutica* colony with a *chamberlini* nest was found there underneath a piece of concrete (50 × 18 × 15 cm).

Altogether we found *chamberlini* in three *mutica* nesting sites, with distances of about 6 m between one other. We could not decide whether the flourishing *mutica* nests belonged to separate colonies, or whether they were parts of a large supercolony. However, two samples of living workers from two similarly adjacent nest sites of another locality (3900 South Street, South Salt Lake City) were successfully mixed and became host of *chamberlini* colony no. 3.

Single *mutica* workers or groups with and without brood were found nearly everywhere in that area when we dug a few centimeters into the soil.

The first site, the southernmost one (Fig. 1), yielded just 30 *chamberlini* workers and intermorphs, but no brood (colony no. 1 in the following). In the second site, about 6 m to the north and beyond the willow brush, we found a *chamberlini* nest (no. 2) about 15 cm below the surface, in the soil and surrounded by larger tunnels with *mutica* workers and brood. The *chamberlini* nest contained larvae and prepupae, about 38 workers and intermorphs, two wingless males, and one male pupa. The prepupae from this colony were used for a karyotype study. In the third site, again about 6 m to the north, in the garbage dump, we found a *chamberlini* nest (no. 3) with about 30 workers and intermorphs, pupae, prepupae, and larvae. One dealate female was detected but escaped capture. The relative importance of intermorphs for our samples is given in table 1 in comparison with Wheeler's data.

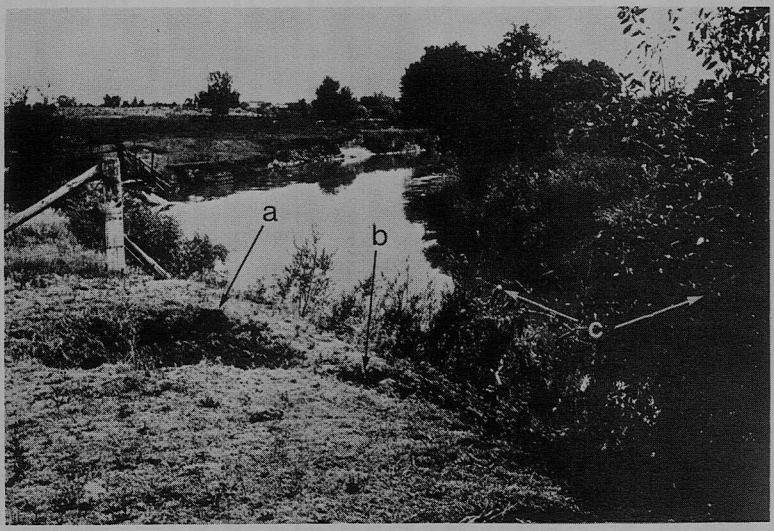

Fig. 1. The *chamberlini* site on the east bank of Jordan River, looking southward (upriver).

a) Site of *chamberlini* colony no. 1 within a *Manica* colony

b) Site of another *Manica* colony which extended along the willow brush to the right

c) willow brush between *chamberlini* colonies 1 and 2

Results of Dissecting *Symmyrmica chamberlini*

The three samples were kept alive for several months. However, numerous specimens died during the first few weeks. A number of them could be dissected following the method described by Buschinger and Alloway (1978).

In a total of 15 ordinary workers without any vestiges of ocelli on their heads, the number of ovarioles was always two, except in one specimen which has three. No spermatheca could be found in any of these workers.

On the contrary, we found five slightly intermorphic specimens, with between one and three more or less perceptible ocelli, with somewhat deeper thoracic sutures, and with 6 ovarioles and a spermatheca each. Two of these specimens, both from colony no. 2 (where males had been present), contained living sperm in their receptacles. Their ovarioles, however, were short and transparent as is usual in young, not yet egg-laying females.

Additional observations were made referring to the abdominal glands of *S. chamberlini*. Thus, the poison gland reservoir was always of usual size and shape, as in other leptothoracine ants. The Dufour's gland, however, is large both in workers and intermorphic females. Its size exceeds considerably that of independent *Leptothorax* species, and it reaches that of, e.g., *Harpagoxenus sublaevis* (Buschinger and Alloway 1978).

A karyological study of 7 prepupae from colony no. 2 was made following the method of Imai et al. (1977). The results, however, were not as good as to permit the presentation of a karyotype. We could only determine the chromosome number, which is $2n = 28$.

Laboratory Observations

We were not able to take large samples of the *Manica* host species with us alive. So only very few observations of interactions between *chamberlini* and their hosts were possible. However, following a method which had already worked with *Formicoxenus nitidulus* (Buschinger 1976), we tried to join *chamberlini* brood and adults with an unnatural host species. We chose a *Leptothorax* species which was nesting within dead willow stems near to our *chamberlini* site. Apparently it represents an unknown, new species belonging to the subgenus *Leptothorax* (= *Mychothorax* Ruzsky). The following experiments and observations were made:

a) After an artificial wintering, four *S. chamberlini* specimens of colony no. 3 were isolated with 5 pupae of the *Leptothorax* species. Honey and freshly killed *Drosophila* were provided. However, the *chamberlini* did not survive. Two agonizing *chamberlini*, almost without movement, were returned to the *Manica mutica* artificial nest arena. The *Manica* workers immediately brought them into the nest, and licked them all over. A few hours later, the two *chamberlini* could feebly walk. Next day, they were running normally in the nest and its arena, having completely recovered. When an apparently dead *chamberlini* was offered to *mutica* workers, they put it in the refuse heap confirming its death. Trophallactic exchange between *chamberlini* nestmates was never seen, but only one was noted between *chamberlini* and *mutica*.

b) The larvae and pupae of colonies no. 2 and 3 were put into a nest together with 20 workers of the *Leptothorax* species mentioned above. One *chamberlini* worker hatched, but died (or was killed?) after two weeks. *Chamberlini* larvae survived an artificial hibernation from 27 October to 1st December 1982. They were easily distinguished from the *Leptothorax* larvae which developed from worker-laid eggs: the *chamberlini* larvae are much hairier.

After the hibernation, the colony raised numerous alate *Leptothorax* males, but no *chamberlini*. The *chamberlini* larvae vanished one after the other.

c) About 20 workers and intermorphs of colony no. 2 were placed together with 25 white and brown worker pupae and a few larvae of the *Leptothorax* species on 1st September, 1982. After one week, the first *Leptothorax* workers had hatched, and 12 *chamberlini* were still alive. Among them an intermorph which had lost the right antenna seemed to become fertile. This specimen, later on, was observed several times to lay an egg. Together with a second intermorph it was still alive on 12 April, 1983.

The first, comparatively long-shaped eggs of *chamberlini* appeared three weeks after the beginning of the experiment. Adult *chamberlini* often fought with each other, possibly in order to eliminate supernumerary reproductives. Some of the victims of these fights were dissected, when they were not too much decomposed. In addition, not only inseminated intermorphs but also ordinary workers died rapidly. After the hibernation (cf. section b), only two *chamberlini* intermorphs were alive, among them the one with only

the left antenna. Both became fertile again, and the brood still contained some hairy *chamberlini* larvae. Between 15 December and 26 January, in a temperature rhythm of 12 hours/15°C and 12 hours/25°C, several *Leptothorax* males, females and workers hatched, but no *chamberlini* larva reached the pupal instar.

After raising the temperature to 10h/17°C and 14h/28°C on 2nd February, 1983, three *chamberlini* larvae became prepupae, and on 10 and 12 March two prepupae molted into apterous male pupae. Nevertheless, it is doubtful whether breeding of *chamberlini* with that *Leptothorax* will be as successful as the experiments with *Formicoxenus nitidulus* and *Leptothorax acervorum* as host species (Buschinger 1976), since both pupae and the remaining prepupa were eaten during the following three days. In the mixed colony *chamberlini*/*Leptothorax* sp. we observed quite amicable relations between the two species. Often the *chamberlini* solicited food from *Leptothorax* workers, and sometimes they were seen licking the mouthparts of larvae. We never saw a *chamberlini* foraging outside the nest, where honey and pieces of *Tenebrio* or *Periplaneta* were offered as food. The *chamberlini* larvae, like those of the *Leptothorax* species, are fed with solid particles of the insect pieces. *Leptothorax* workers place the particles on the ventral surface of the larvae, which then chew and eat them.

Discussion

Our knowledge of the biology of this rare ant still remains fragmentary. We can confirm the observation of Chamberlin, as reported by Wheeler (1904) in that we also found this ant in mixed colonies with *Manica mutica,* in the flood-plains of Jordan River near Salt Lake City. The guest ants are living within independent nests in the midst of prosperous *Manica* colonies. However, we could not observe whether they solicit food from their hosts, or what are the other relations of the two species. The observation mentioned in the previous section, experiment a, raises questions of whether the licking of *chamberlini* by the *mutica* hosts is linked to any important cuticular secretion.

The nesting habits of *S. chamberlini* resemble closely those of *Leptothorax provancheri,* the guest ant of *Myrmica incompleta* Provancher (Buschinger et al. 1980). As was already suggested by

Table 1. Ratios of workers and intermorphs in colonies of *Symmyrmica chamberlini*

Source	Workers (%)	Intermorphs (%)	Total
Wheeler (1904)	8 (38)	13 (62)	21
Colony no. 1	20 (66)	10 (33)	30
Colony no. 2	16 (42)	22 (58)	38
Colony no. 3	13 (43)	17 (57)	30
Σ	57 (48)	62 (52)	119

Wheeler (1910), *S. chamberlini* is closely allied to the genus *Formicoxenus,* guest ants of *Formica* species in Europe and North America. Since the wingless male of *chamberlini* nevertheless is not as workerlike as the *Formicoxenus* male, Wheeler may be right in suggesting that it could represent an archaic form of *Formicoxenus.*

The close relationship of *S. chamberlini* and *Formicoxenus* is further corroborated by our observations of intermorphic queens in our new material. Such queens, which often look like ordinary workers except that they have one or up to three vestigial ocelli and sometimes a little bit more developed thoracic sutures, occur quite frequently in *Formicoxenus nitidulus* (Buschinger and Winter, 1976), in *F. hirticornis* (Buschinger, 1979), and in *Leptothorax provancheri* (Buschinger *et al.* 1980). We cannot yet determine whether *S. chamberlini* also has a functional monogyny like the 3 guest ants we mentioned above. This would mean that alongside one functional queen in each nest, there exists one or several inseminated but not egg-laying potential queens. However, at least our finding of two recently inseminated intermorphic females in *S. chamberlini* colony no. 2 reveals that, as in the other guest ants, copulation takes place within or near the mother colony, and that newly mated females may remain for a while in the mother nest.

The analysis of intermorph composition presented in table 2 based on the classification of Plateaux (1970) for caste polymorphism in *Leptothorax nylanderi,* revealed only few superior intermorphs with intermediate trunk between a fully developed gynomorph and a typical ergatomorph. Moreover the inferior intermorph classes seem to be dominated by the form 4 which has 3 small or minute ocelli in any combination, a mesothorax not, or slightly enlarged, a promesonotal suture more or less prominent. The individuals with a potential or actual queen function capacity are found

Table 2. Types of *S. chamberlini* intermorphs according to Plateaux' classification of *Leptothorax nylanderi*.

Source	Form 2	Form 3	Form 4	Form 6–7	Total examined
Wheeler (1904)	0	1	5	0	6
Colony no. 1	3	1	4	2[+])	10
Colony no. 2	7	0	13	2[++])	22
Colony no. 3	2	2	13	0	17

[+])Both with thoracic sutures and sclerites according to Plateaux' form 7, except for the lack of wings. One specimen with very short forewing rudiments.
[++])Two specimens between Plateaux' form 6 and 7, without traces of wings.

mainly in that class of intermorphs. It is worthy to stress that Holliday's (1903) data for 1000 specimens of *L. provancheri* includes 37% of intermorphs without the microgynes; the intermorph composition exhibits the same trends as in *chamberlini*.

The karyotypes cannot yet confirm a closer relationship of all these guest ants. However, they also do not contradict such an assumption. *F. nitidulus* has a haploid number of n = 15 chromosomes, *L. provancheri* has n = 11, and *S. chamberlini* with n = 14 lies in between. For *F. hirticornis* and *diversipilosus* the chromosome numbers are not yet known.

Summing up the known features, queen polymorphism with alate and intermorphic females, males with their tendency to reduce wings and to become ergatomorphic, the presence of inseminated young (and in *Formicoxenus* also old) potential queens in the nests, and the life habits as guest ants, we believe that *Symmyrmica,* and also *L. provancheri,* should be incorporated in the genus *Formicoxenus*. A comparative morphological study has been undertaken in order to link the biological informations accumulated on the guest ants mentioned above in a taxonomic revision of the genus *Formicoxenus*.

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Summary

Symmyrmica chamberlini was described by Wheeler (1904) from specimens taken by C.V. Chamberlin in 1902 in a colony of *Manica mutica* (Emery) near Salt Lake City. No further records of this species are known. In order to find out the systematic relations of *Symmyrmica* to other ants like *Leptothorax provancheri* Emery or those of the genus *Formicoxenus,* we have collected some new material in August 1982, in the Salt Lake City area. The morphology, female polymorphism, and wingless male together with biological features indicate that *S. chamberlini* is a species that should belong to the genus *Formicoxenus.*

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